

Weakly Chaotic Population Dynamics in Random Ecological Networks

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Abstract

Population dynamics in random ecological networks are investigated by analyzing a simple deterministic equation. It is found that a sequence of abrupt changes of populations punctuating quiescent states characterize the long time behavior. An asymptotic analysis is developed by introducing a log-scaled time, and it is shown that such a dynamical process behaves as non-steady weak chaos in which population disturbances grow algebraically in time. Also, some relevance of our study to taxonomic data of biological extinction is mentioned.

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Almost all possible equilibrium populations in random ecological networks become unstable when the number of fully connected species is sufficiently large [1–3]. This is a general result obtained from random matrix theory [1]. The loss of stability of equilibrium populations, of course, does not necessarily imply a catastrophe of the system; it is known that limit cycles, heteroclinic cycles, and chaos arise beyond the loss of the stability in a few species system [4–7]. Therefore, it seems natural to consider how populations evolve in ecological systems consisting of many randomly interacting species.

This problem is related to the co-evolution of many species in an unchanging physical environment. Each species evolves in the effective environment formed by the others, and the evolution of one species alters the environment of many others. This leads to a kind of frustration in the ensemble of species, and if the frustration is never resolved by the evolution, it would continue indefinitely. Such a scenario was proposed by Van Valen [8] and is often referred as the Red Queen hypothesis [7,8].

Our aim is to present significant features of population dynamics in a random ecological network by analyzing suitable mathematical models. The choice of models may be a controversial step, and various types of dynamical behavior will be observed depending on this choice. We postpone discussion about this step, and in this paper we focus on a specific model which is composed of simple deterministic equations for the populations of N species. The equations are so simple that we can employ an asymptotic analysis for a long time behavior of the populations.

Our equations describe the time development of populations $\{x_i\}$ of N species. We assume that each species grows at a rate λ_i which is expressed by a Lotka-Volterra type coupling with the other species:

$$\lambda_i = a_i + \sum_j g_{ij}x_j, \quad (1)$$

where a_i and g_{ij} correspond to an intrinsic growth rate and competing coefficients, respectively. We further assume that each population has a saturation level, and we normalize the populations so that $x_i = 1$ at the saturation levels. x_i then obeys the logistic equation:

$$\frac{dx_i}{dt} = \lambda_i(x_i - x_i^2), \quad (2)$$

where $0 \leq x_i \leq 1$, and $x_i = 0$ and $x_i = 1$ correspond to 'extinction' and 'saturation', respectively. Although we consider the case that $a_i = 0$ in (1) for simplicity, the analysis given below is easily extended so as to include this term. From our motivation, N is a given large number, and g_{ij} is assumed to be a random variable obeying a Gaussian distribution with zero mean and deviation J/\sqrt{N} except for $g_{ii} = 0$. Note that the value of J can be renormalized to 1 by changing the time scale.

Equation (2) has 2^N equilibrium states, each of which is expressed by $(x_1, x_2, \dots, x_N) = (\sigma_1, \sigma_2, \dots, \sigma_N)$, where $\sigma_i \in \{0, 1\}$. In an equilibrium state $(\sigma_1, \sigma_2, \dots, \sigma_N)$, species satisfying $\sigma_i = 1$ exist at their saturation levels, while other species are all extinct. We call the special state with $x_i = 0$ for all i 'perfect extinction'. The linear stability of equilibrium states is determined by the eigenvalues of the linearized equation around these states. It can be easily shown that the probability of choosing a stable state from all equilibrium states equals $1/2^N$, and therefore almost all equilibrium states correspond to saddle points. Although the expectation of the number of stable equilibrium states is approximately 1, whether or not a given system can reach such a state depends on the global structure of the flow in phase space.

We first give results of numerical simulations of (1) and (2) in Fig. 1. It is seen that a population abruptly increases or decreases from a quiescent state close to an equilibrium. We call the quiescent state and abrupt change 'quasi-equilibrium' and 'burst', respectively. Such dynamical behavior seems to continue indefinitely within our computationally available time. In fact, even if the system eventually settles into a stable equilibrium, a long transient time is needed to reach the neighborhood of this state. We can estimate the waiting time as $O[\exp(2^N)]$, because the system needs to experience $O(2^N)$ bursts to meet the stable equilibrium state, and the time interval between two successive bursts grows exponentially on the average. (The latter statement will be demonstrated in the argument below.) We thus focus on the long time behavior composed of 'quasi-equilibrium' and 'burst' irrespective

of the final state.

Now, we develop a new asymptotic method. Our key idea is to introduce a new variable y_i defined as to satisfy

$$x_i = f(y_i) := \frac{\exp(y_i)}{1 + \exp(y_i)}. \quad (3)$$

Then, Equation (2) is transformed into a simple form:

$$\frac{dy_i}{dt} = \lambda_i. \quad (4)$$

Integrating this equation, we obtain

$$y_i(t) = y_i(0) + \langle \lambda_i \rangle t, \quad (5)$$

where $\langle \lambda_i \rangle$ is the average of the growth rate over the time interval from 0 to t and is written as

$$\langle \lambda_i \rangle = \frac{1}{t} \int_0^t dt' \lambda_i(t'). \quad (6)$$

Since $\langle \lambda_i \rangle$ does not converges to zero for $t \rightarrow \infty$ except in the case that the system approaches the perfect extinction, we obtain the asymptotic form of x_i for $t \rightarrow \infty$:

$$x_i(t) = f(y_i(0) + \langle \lambda_i \rangle t) \rightarrow \theta(\langle \lambda_i \rangle). \quad (7)$$

That is, after a sufficiently long time, the system stays at a quasi-equilibrium state, and whether x_i is close to 0 or to 1 is determined by the sign of $\langle \lambda_i \rangle$. We say, in this sense, that the dynamics of the population is slaved to that of the average growth rate. We thus consider time development of $\langle \lambda_i \rangle$. The definition of $\langle \lambda_i \rangle$ given by (6) leads immediately to the equation:

$$\frac{d\langle \lambda_i \rangle}{dt} = \frac{1}{t} (-\langle \lambda_i \rangle + \sum_j g_{ij} x_j), \quad (8)$$

where we have used the expression of the growth rate (1). Then, by introducing a log-scaled time $\tau = \log(t)$, defining a new variable $h_i(\tau) = \langle \lambda_i \rangle$, and using the asymptotic form (7), we obtain the equation describing the slow dynamics of the average growth rate:

$$\frac{dh_i}{d\tau} = -h_i + \sum_j g_{ij}\theta(h_j). \quad (9)$$

Here, it is worth noting that the equations of motion for the average growth rates are autonomous when we use a log-scaled time τ . We now consider the relationship between the orbits of $h_i(\tau)$ and $x_i(t)$. First, from the asymptotic form (7), x_i is close to 0 or 1 depending on the sign of h_i , and a burst of the i -th species is identified with a zero-crossing of h_i . Second, consider periodic motion of h_i expressed by $h_i(\tau) = \sin(2\pi\tau/T)$. Then, a log-scaled time at which h_i crosses zero for the n -th time is given by $\tau_n = Tn/2$. Correspondingly, zeros of $\langle \lambda_i \rangle$ occur at $\exp(Tn/2)$. This means that the time interval between two successive bursts grows exponentially in n . We can see in general that a periodic orbit of $h_i(\tau)$ corresponds to a transient orbit of $x_i(t)$ attracting to a heteroclinic cycle. Finally, the long time behavior of populations corresponding to chaotic motion of h_i is described by a non-steady process of an irregular occurrence of bursts. The time interval between two successive bursts grows irregularly in n , but on the average grows exponentially.

We also note that Equation (9) has a form similar to the random neural network model proposed by Sompolinsky et.al. [9] which is obtained when we replace $\theta(h_j)$ by $\tanh(Kh_j)$. They studied the statistical properties of fluctuations by developing a new method called 'dynamical mean field theory' and showed that their equation exhibits chaotic behavior when $KJ > 1$ in the limit $N \rightarrow \infty$ [9]. Therefore, one may guess that (9) has chaotic solutions for sufficiently large N .

In order to investigate dynamical properties of solutions $h_i(\tau)$, we performed numerical simulations of (9). Noting that the equation is piece-wise linear and discontinuous at $h_i = 0$, we can construct a solution starting from an initial condition $\{h_i(0)\}$ in the following way. First, the equation (9) can be integrated analytically until a time τ_1 at which the first burst occurs, and $h_i(\tau_1)$ is expressed by

$$h_i(\tau_1) = (h_i(0) - \lambda_i) \exp(-\tau_1) + \lambda_i, \quad (10)$$

where $\lambda_i = \sum_j g_{ij}\theta(h_j)$ takes a constant value during this period, and τ_1 is given by

$$\tau_1 = \text{Min}_i \log(1 - \frac{h_i(0)}{\lambda_i}), \quad (11)$$

where the index i runs over the species satisfying $h_i(0)\lambda_i < 0$. By repeating a similar procedure, we obtain a sequence of τ_i with $(i = 1, 2, \dots)$, and simultaneously the solution of (9).

In Fig. 2, we plotted the species which bursts at τ_i with $(i = 1, 2, \dots)$. The plotted pattern seems to be random along the time axis, but certain inhomogeneity in species can be seen. In fact, Fig. 3 shows that the time interval between two successive bursts obeys a Poisson distribution $P(\tau)$, while as shown in Fig. 4, $Q(\tau)$, the distribution of persistence time of positive h_i , has a power law tail

$$Q(\tau) \sim \tau^{-2} \quad (12)$$

for $\tau \rightarrow \infty$, which is due to the randomness of the long-time average of h_i . Therefore, in the random neural network model proposed by Sompolinsky et.al. [9], similar behavior is never observed [11]. From the forms of these distributions, we can expect that the dynamics of $h_i(\tau)$ are steady. As a result, on the real time scale, the population dynamics are non-steady; the time interval between two successive bursts grows in n irregularly, but on the average exponentially. Further we numerically calculated the maximum Lyapunov number μ for many set g_{ij} chosen randomly, and found this number to be positive in each case. Thus, a disturbance $\delta h_i(\tau)$ grows as $\delta h_i(\tau) \sim \exp(\mu\tau)$, that is, time series of $h(\tau)$ are orbitally unstable. This result leads to power law divergence of a disturbance of populations $\delta x_i(t)$ of the form

$$\delta x_i(t) \sim t^\mu, \quad (13)$$

and thus zero Lyapunov exponents. Our population dynamics therefore are not chaotic, but 'weakly chaotic' [10]. Discussion of the distribution function of μ for the ensemble of $\{g_{ij}\}$, the Lyapunov spectrum, their dependence on N , and a proof of (12) will be presented in a separate paper [11].

We have shown the significant features of the long time behavior of populations described by (1) and (2). These are expected to be common to a large class of models of random ecological networks. Recently, population dynamics in random ecological networks have been studied by analyzing another type of equation [12,13]. This equation is obtained by normalizing the sum of the populations to unity, and the resultant form is the same as the replicator model proposed in the context of molecular evolution [4,6]. We have found that a non-steady process with a log-scaled time appears generally in a random network [14], and one of the authors has investigated a transition to 'chaos with a log-scaled time' in a four dimensional system [15].

Here, we present a remark: a small perturbation of the dynamical system, e.g., the addition of $\epsilon F(x_i)$ to the right-handed side of (2), yields topologically unequivalent orbits $x_i(t)$. In other words, the above solutions are structurally unstable. This structural instability is analogous to that of homoclinic orbits [16]. Since structurally unstable behavior cannot be observed without certain constraints, one may object that the behavior we study is not generic. We believe however that an understanding of the behavior of the unperturbed system will provide the first step toward understanding the rich variety of dynamical phenomena of perturbative systems much as center manifold theory has succeeded in describing complex behavior near bifurcation points [16].

We finally discuss the relevance of our study to the taxonomic data of biological extinction. According to Van Valen [8], the lifetime of species obeys a Poisson distribution with an extinction rate Ω which is about 10^{-7} [year $^{-1}$]. (Such a simple picture has been called 'continuous extinction'. The alternative to this is the 'episodic extinction' picture [17].) Since extinction ($x_i = 0$) never occurs in our model, we need to introduce another assumption in order to see the correspondence with extinction in taxonomic data. One plausible idea is to regard an abrupt decrease of a population from near the saturation level as extinction. This may be justified, because the taxonomic data are made from fossil records. Then, noting that the time spent near the saturation level measured with a log-scaled time corresponds to the persistence time of positive h_i , we find that the lifetime of a species obeys the dis-

tribution $Q(\tau)$. This result seems to be inconsistent with the taxonomic data, because our lifetime is measured by a log-scaled time. The apparent paradox is resolved by taking a small perturbation into account. In fact, we can show that a certain class of perturbations alters the expression of the scaled time τ from $\tau = \log(t)$ to $\tau = \epsilon t$ while keeping the τ dependence of statistical expressions unchanged [11]. ϵ here measures the slowness of the time scale which is related to the magnitude of the perturbation. A similar change of a time scale is observed at a global bifurcation called a 'saddle connection' [16].

In order to present more concrete discussion, we adapt [year] as the time unit of the population dynamics and set $\epsilon = 10^{-6}$ as a typical value. Then, our result implies that (1) for species shorter lived than about 10^7 [year] extinction occurs randomly with respect to the age of the species at a constant rate of about 3×10^{-7} [year $^{-1}$], and (2) for species much longer lived than about 10^7 [year], older species have a smaller probability of extinction. The first result agrees with the taxonomic data of Van Valen [8]. Also, there are some taxonomic data consistent with our second result [8,17], though we have not checked the power law distribution for the lifetimes of longer lived species. According to our interpretation, the time scale of extinction is determined by slowness of small perturbations for population dynamics. We must consider what factors introduce the most relevant perturbations so as to estimate the value of ϵ . Mutations of genes may be one candidate. It would be interesting to study the population dynamics of a system taking into account the effect of mutations [18–20].

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FIGURES

FIG. 1. Time development of populations of $N = 256$ species. All populations within $[0.01, 0.99]$ are plotted every time unit. An initial condition was chosen randomly. An Euler method with a time mesh of 0.1 was adapted in the numerical simulation.

FIG. 2. Plot of bursts in a species- τ plane after 10000 bursts starting from an initial condition chosen randomly.

FIG. 3. Distribution of intervals between two successive bursts for $N = 256$ species. The distribution is made from data of 40000 bursts after discarding the initial transient behavior. The distribution curve is well-approximated as $P(\tau) = \alpha \exp(-\alpha\tau)$, where $\alpha = 25$. α would increase linearly with N .

FIG. 4. Distribution of persistence time of positive h_i . The distribution is made from data of 80000 bursts after discarding the transient. The distribution curve has a power law tail for $\tau > \tau_c$, while it is consistent with a Poisson distribution for $\tau < \tau_c$. The cross-over time τ_c is about 10.







